Differences in the spawning migration and river catchment use of Atlantic salmon and sea trout in a multiple stock river: telemetry-derived insights for management

N. R. Gauld[a,b], R. N. B. Campbell[b], M. C. Lucas[a]

[a] School of Biological and Biomedical Sciences, Durham University, South Road, Durham, UK, DH1 3LE

[b] The Tweed Foundation, Drygrange Steading, Melrose, TD6 9DJ, UK

Corresponding author: N. R. Gauld, School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, UK

Email address: n.r.gauld@gmail.com

Abstract

Management of multiple exploited stocks of anadromous salmonids in large catchments requires understanding of movement and catchment use by the migrating fish and of their harvesting. The spawning migration of sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) was studied in the River Tweed, UK, using acoustic telemetry to complement exploitation rate data and to quantify catchment penetration. Salmon (*n*=79) and sea trout (*n*=65) were tagged in the tidal Tweed in summer-autumn. No tagged salmon left the river before spawning, but 3% (2010) and 8% (2011) of pre-spawning sea trout dropped out. Combined tag-regurgitation/fish mortality in salmon was 12.5%, while trout mortality was 6% (2010) and 0% (2011). The estimated spawning positions of salmon and sea trout differed; tagged salmon were mostly in the main channel while trout occurred mostly in the upper Tweed and tributaries. Early fish migrated upstream slower than later fish, but sea trout moved through the lower-middle river more quickly than salmon, partly supporting the

hypothesis that the lower exploitation rate of trout (1%, vs 3.3% for salmon) there is by differences in migration behaviour. This study illustrates the utility of telemetry in exploring differences in catchment use and exploitation patterns of multiple stocks.

Kewords: *Salmo salar*; *Salmo trutta;* migration; telemetry; spawning; stock

Introduction

Large catchments provide potentially wide distributions of spawning and nursery habitats to anadromous fishes and the distribution, and resultant use, of these, depends on the geomorphology of the catchment and of associated hydrological, chemical and biological processes (Davey and Lapointe 2007; Fausch et al. 2002; Scarnecchia and Roper, 2000). Combined with philopatric behaviour, in migratory fish species, this often results in distinct stock structuring and associated ecological responses, especially in large catchments (Primmer et al. 2006; Schaller et al. 1999; Stewart et al. 2002). Where exploited multi-species and/or mixed-stock salmonid communities occur, for example in many European rivers that contain anadromous Atlantic salmon (*Salmo salar)* and sea trout (*Salmo trutta)*, management is contingent upon understanding the movement of returning adults to, and utilisation of, spawning and rearing habitats within the catchment as this has major influences on the distribution and production of juveniles (Finstad et al. 2010; Finstad et al. 2013; Foldvik et al. 2010).

The occurrence of pronounced spawning migrations by many migratory fishes, including salmonids, is a reflection of the restricted spatial and temporal distribution of opportunities for reproduction in those populations (Lucas and Baras 2001). However, the timing, rate of movement and spawning sites may vary widely; adult Atlantic salmon and sea trout often migrate substantial distances up the main channel and into tributaries, (Finstad et al. 2005; Laughton and Smith 1992; Östergren et al. 2011), but can also spawn just a few kilometres from the sea in the main channel (e.g. Laughton & Smith 1992). Atlantic salmon and sea trout migration after river entry comprises several behavioural stages; the migration stage, the searching stage and the holding stage (Bagliniere et al. 1990; Hawkins and Smith 1986; Økland et al. 2001; Thorstad et al. 2008). The initial migration stage is when most upriver movement occurs and can last from a week to over a month, with the duration of the stage depending on migration distance (Bendall et al. 2012; Finstad et al. 2005; Økland et al. 2001). During this period fish tend to sustain constant upstream movement rates, regardless of flow and time of day. Stepwise upstream movements begin after the first stop, after which movement is usually but not always restricted to crepuscular and nocturnal periods (Bagliniere et al. 1991; Kennedy et al. 2013; Laughton 1989; Webb 1989; Webb 1990). The number of halts in migration progress tends to increase with migration distance (Økland et al. 2001).

Increasingly, in the UK and more widely, exploitation for European anadromous salmonids within rivers is by recreational rather than commercial means (e.g. Butler 2009; Cefas-EA-NRW 2014) and understanding the levels and patterns of exploitation is fundamental to effective management and conservation of these species and stock elements (Bunt 1991; Gee 1980; Potter et al. 2003; Thorley et al. 2007). In the River Tweed, UK, both Atlantic salmon and sea trout provide major recreational fisheries (Sheail 1998), but a T-bar tagging study in the lower river over the period 1994 to 2011 (Tweed Foundation, 2015a) found pronounced differences in exploitation pattern within the catchment (Table 1), and a 2.5-fold lower reported exploitation rate of sea trout, especially in the lower-middle river (3.5-fold difference). Multiple factors affect the catchability of salmonids (Bunt 1991), but understanding the migration behaviour and availability of differing stock components to exploitation can aid the interpretation of more conventional exploitation data and improve its value for fisheries management purposes (Metcalfe & Pawson, 2004). We hypothesized that the different patterns in observed exploitation between autumn run trout and salmon in the Tweed are due to altered availability of sea trout resulting from different migration speeds through the heavily fished lower and middle reaches. We also sought to evaluate the levels of non-angling losses and rates of exit from the river of tagged salmon and sea trout tagged, to improve the precision of estimated angling exploitation rates. Lastly, we hypothesised that autumn-run tagged salmon and sea trout spawn in different areas of the catchment.

Study area

The study was carried out on the River Tweed in south-eastern Scotland and north-eastern England, which drains west to east and empties to the North Sea. The Tweed is the sixth largest river in mainland Britain, the second largest in Scotland and has some of the largest Atlantic salmon and sea trout populations in the UK (Gardiner, 1989; Sheail, 1998). The fisheries in the Tweed are of high socio-economic value to the Scottish Borders and north Northumberland. A report for the River Tweed Commission found the fisheries to be worth £18.2 million to the local economy and to support 496 full time job equivalents (SQW Ltd 2006). The Tweed catchment covers 5000 km^2 with an estimated 2160 km of the main channel and tributaries accessible to anadromous fish (Gardiner, 1989). The main channel of the Tweed is 156 km in length with the main tributaries the Ettrick Water, Gala Water, Leader Water, River Teviot, River Till and River Whiteadder being; 53, 36, 22, 60, 73, 59 km respectively. The mean discharge for the Tweed is 80.9 m^3s^{-1} with the main tributaries the Ettrick Water, Gala Water, Leader Water, River Teviot, River Till and River Whiteadder being; 15.3, 3.7, 3.4, 20.6, 8.5, 6.7 m^3s^{-1} respectively. The Tweed basin is a drumlin field, formed during paleo-icestreams (Everest et al 2005). The water quality of the river is very high, with there being very little pollution (Currie, 1997), although nutrient enrichment can still be a problem. The River Tweed is a designated Site of Special Scientific Interest (SSSI) within the UK and is an EU Natura 2000 Special Area of Conservation (SAC) for Atlantic salmon and lampreys. Compared to many rivers, there are relatively few anthropogenic impacts and the hydrology, although modified, is, to a considerable degree, unregulated.

Methods

The movement rates and fate of salmon and sea trout adults tagged in the tidal reaches from summer, through to autumn were studied by telemetry. Acoustic telemetry was chosen rather than radio telemetry as the fish were tagged in the tidal area of the River Tweed and dropouts from the river catchment were monitored in the saltwater estuary, conditions where radio telemetry has poor range and detectability (Lucas & Baras 2001).

Acoustic monitoring receiver locations

Seventeen Acoustic Monitoring Receivers (AMR) (Vemco VR2 and VR2W, Vemco, Bedford, Nova Scotia, Cananda) were positioned along the River Tweed, its estuary and in major tributaries, in relatively deep and quiet water. Two receivers were placed in the estuary to cover both the inner and outer estuary zones so that tagged fish dropping out to sea could be recorded. Main stem AMR positions were placed approximately every 11 km along the River Tweed upstream from the estuary to the upper Tweed at Fairnilee, a distance of 86 km (Fig. 1). Tributary AMRs were placed a short distance inside each of the major tributaries of the Tweed; Whiteadder Water, River Till, River Teviot, Leader Water, Gala Water and Ettrick Water (Fig. 1). Tributary AMRs were placed out of tag range from the mainstem but before any sub tributaries. All AMRs were range tested by passing test tags at different ranges past the loggers and detection rates calculated; in tests, these efficiencies averaged 97%. Effective ranges of the receivers exceeded 100 m in normal flow conditions, although it is conceivable that range reduced during high flows. The Tweed is widest at Tweed AMR 1 with a river width of approximately 100 m, as a result two receivers were deployed on opposite sides to achieve coverage. Three incidences occurred where a fish was not detected by a receiver but was detected by subsequent AMR positions, this equates to a 1.7% chance of fish not being detected.

Fig. 1 here

Adult fish capture

Fish were captured on various dates in 2010 and 2011 at Paxton, within the area of tidal influence (Fig. 1) and tagged (Table 2). Netting was carried out at approximately the time of the head of the flood tide on each date. Fish were captured by commercial fishermen using a seine net deployed by a rowing boat and retrieved at the bank. As soon as the net was brought in, selected captured untagged fish were transferred to aerated holding tanks on the bankside. Only a small proportion of the netted fish were telemetry tagged, all of which were selected for being in prime condition. Netting dates were determined by the availability of the commercial netting teams as their time needed to be bought and usable dates were limited. Netting dates were spread to maximise the range of months in which fish were tagged but could not result in fish being tagged across all months due to the limited netting seasons and a moratorium on netting before May, brought in to reduced exploitation of spring-migrating salmon. However, fish were netted in October after the commercial netting season ended under scientific licence.

Atlantic salmon intragastric tagging procedure

Atlantic salmon were anaesthetised by transferring them to an induction tank containing phenoxyethanol (0.3 ml L^{-1}) and river water until they became unresponsive to external stimuli, lost equilibrium and their ventilation rate reduced. Once a fish was anaesthetised it was transferred to a measuring board where the fork length (mm) was measured and a scale sample taken. A uniquely numbered T-bar anchor tag was inserted into the musculature below the dorsal fin for external identification of the fish. The fish was then intra-gastrically tagged, since this method is regarded as suitable for adult salmon (Smith et al. 1998). Adult Atlantic salmon do not feed after returning to rivers and regurgitation rates are normally low (Smith et al. 1998). An acrylic tube with a rounded end was carefully inserted down the oesophagus, an acoustic tag (Models LP-7.3, LP-9, LP-13, Thelma Biotel AS, Trondheim, Norway; details and dimensions given in Table 3) was then placed in the tube and inserted into the stomach by carefully pushing it down the oesophagus with a plunger.

The plunger was slowly removed from the oesophagus and the mouth and oesophagus was inspected to confirm tag placement. After the procedure the fish was placed in a container filled with highly aerated water for recovery. Once the fish regained equilibrium, displayed healthy gill ventilation and reacted to external stimuli it was released back in to the river at point of capture. The gastric tagging procedure from administration of anaesthetic to re-release in the river typically took five minutes to complete. All gastric tagging procedures were carried out by R. Campbell under the husbandry and management exclusion clause of the Animals (Scientific Procedures) Act 1986.

Sea trout intraperitoneal tagging procedure

Surgical tagging was opted for in sea trout due to high tag regurgitation rates in prior studies (Gerlier and Roche 1998). After anaesthesia induction, as described above, he fish were measured, T-bar tagged and placed on a V-shaped surgical table. A tube was inserted in to the mouth and a dilute concentration of phenoxyethanol (0.15 ml L^{-1}) was run over the gills for the first period of the procedure before the supply was changed to 100% river water near completion of the procedure. An incision was made on the ventral side of the fish anterior to the pelvic girdle before a disinfected (immersed in 96% ethanol for several minutes, then allowed to dry in a clean environment) acoustic transmitter (Models LP-7.3, LP-9, LP-13, Thelma Biotel AS, Trondheim, Norway) was inserted in to the body cavity. The incision was closed with between three to five independent absorbable sutures (3-0 Vicryl rapide, Ethicon Ltd, Livingston, UK) dependent on incision size. Recovery and release was carried out as described above. All procedures were carried out by M.C Lucas and N.R Gauld under UK Home Office License. Details of the fish captured and tagged and of the tag mass to body mass ratio are presented in Online Resource 1.

Tracking

The section of river between the first river acoustic listening station (Tweed AMR 1; Fig. 1) and the estuary listening station array was tracked by boat (with an outboard motor) using a mobile acoustic receiver and directional hydrophone VR100 Acoustic tracking receiver and VH110 directional hydrophone; Vemco, Bedford, Nova Scotia, Canada) on multiple occasions per year (15 trips in 2010 and 10 in 2011) during the study periods (June to November). The boat was launched just below the AMR and driven at low throttle down the river at a speed less than 100 m per minute to ensure low acoustic noise and to minimise the risk of missing acoustic tags by moving through their reception zone too fast. The directional hydrophone was slowly rotated from the front of the boat allowing the operator to sweep across the river, checking for tags. As soon as the first signals from an acoustic tag coding sequence were detected the boat's engine was stopped and the hydrophone was manoeuvred until the tag sequence was detected again. Once the full tag sequence was detected and logged on the tracking unit the boat engine was restarted and movement down river was recommenced. Manual tracking was also done from the bank, by wading, at key localities, particularly near the release site on a weekly basis during the tagging period and on a fortnightly basis thereafter.

AMR data retrieval

Data retrieval and maintenance was carried out on a weekly basis for loggers in the mainstem of the River Tweed. Data retrieval from tributary loggers was carried out on a fortnightly basis as they were expected to fill with data less quickly. Maintenance and data retrieval on the two estuary loggers was carried out monthly basis due to access limitations, but loggers were always functional and with free data storage space upon retrieval.

External data retrieval

Data for the volumetric flow of the River Tweed at; Boleside, Sprouston, and Norham as well as the Scottish tributaries; Ettrick Water (at Lindean), Gala Water (at Galashiels), Leader Water (at Earlston), Teviot Water (at Ormiston Mill) and Whiteadder Water (at Hutton Castle) was received from the Scottish Environment Protection Agency (SEPA) (Fig. 1). Flow data for the River Till (at Wooler) was provided by the Environment Agency (EA) (Fig. 1).

Estimations of regurgitation or mortality

One of the problems with intragastric tagging is the possibility of regurgitation, another difficulty is interpreting which tags are potential regurgitates. For the purpose of this study we removed any tags from the analysis that appeared to be regurgitates or mortalities. Regurgitates/dead fish (salmon) and dead fish (sea trout) were deemed as tags that were found in the same location for over two months, whether by manual tracking or constant presence in the vicinity of an AMR, and where no subsequent upstream or downstream detection was recorded within the tracking period.

Statistical analysis

Net movement rates for migrating fish were calculated using logged AMR data, whereby time delay and distance between stations were used to calculate groundspeed, which was calculated as body lengths per second rather than kilometres per hour to compensate for size variation within the sample groups. Data from tags believed to have been associated with regurgitation or fish mortality were not included in analyses from the time at which regurgitation/mortality was detected by retrospective track reconstruction. Flow data during migration was calculated for each fish by calculating the mean flow during the period between each pair of AMR positions using 15 minute flow records collated by SEPA/EA for the nearest gauging station upstream. General Linear Mixed effects Models (GLMMs) were used to analyse the variation in groundspeeds. Models included the following factors; species; year; river section and river reach. Covariates included log river flow, as well as release date (day of year) and interaction terms between log flow and species and log flow and year. Fish ID was used as a random factor to account for any effects of pseudo-replication caused by using multiple records of the same fish. A base model that included all variables was created initially. Multiple variants of this were then run with individual or multiple variables excluded. The GLMMs were calculated in the statistical package R (R Core Team 2012) using the lme4 package (Bates et al. 2014) and the lmeTest package (Kuznetsova et al. 2014). Model assumptions were met as there were linear relationships between predictors and responses; residuals were normal and displayed homoscedasticity.

Model selection was based on the Akaike Information Criterion (AIC)(Akaike, 1998). The model with the lowest AIC score was initially selected as the candidate model. However, model selection was expanded using the criteria described by Richards (2008), whereby all simpler variants of the candidate model with a Δ-value lower than 6 were also considered. However, for the purpose of species comparisons simpler models that retained species were opted for over the simplest models without species.

Results

In total, 79 Atlantic salmon (51 in 2010, 28 in 2011) and 65 sea trout (33 in 2010, 32 in 2011) were tagged at Paxton. During both study seasons there were high rates of fish detection after release with 88% (45) and 79% (22) of Atlantic salmon and sea trout tags respectively being detected up to 14 weeks after tagging ceased in 2010. Rates of detection were also high in 2011 with 82% (27) of Atlantic salmon and 100% (32) of sea trout being detected after tagging and release with tag detections continuing for up to 16 weeks after tagging ceased. There was an estimated total regurgitation/mortality rate of 12.5% (9.6% (4 fish) in 2010 and 17.8% (5 fish) in 2011) for salmon tags located via manual tracking and fixed AMRs in the lower Tweed in both years combined. For comparison there was an estimated 6% (2 fish) mortality rate for sea trout in 2010 and no evident mortalities in 2011. Two acoustic tagged salmon and one sea trout were caught by anglers in 2010 but none in 2011 In a concurrent exploitation rate study carried out by the Tweed Foundation using conventional T-bar tags, two salmon and four sea trout were caught in the catchment by anglers in 2010 and two salmon and one sea trout in 2011 (Tweed Foundation 2015a). However total angler catches for salmon were 23,219 in 2010 and 16,682 in 2011 and sea trout were 2,621 in 2010 and

2,499 in 2011. These salmon catches were the best and second best totals ever for the river indicating very large runs of fish and therefore reduced probability for any individual to be caught.

As well as pre-spawning sea trout migration, post-spawning sea trout kelt migration was also recorded in both years. One (3%) and seven (21.8%) of the tagged adults were recorded moving downstream, post-spawning, in 2010 and 2011 respectively. This movement occurred as early as November 18th 2011 and as late as January 29th 2012. Two of the sea-trout conventionally tagged in 2010 were caught in the sea off the English coast to the south of the Tweed in 2011. Based on sexing during tagging there was a 3:4 male to female sex ratio among sea trout kelts.

Sea trout and Atlantic salmon migration destinations 2010-2011

The last known location for each migrant was determined through a combination of fixed AMR records as well as manual tracking. Any fish tag released in the Tweed, but which then quickly descended the river and left the estuary was defined as a 'dropout'; none occurred for Atlantic salmon (Fig. 2) while for sea trout dropout rates were 8% (2) and 3% (1) in 2010 and 2011 respectively (Fig. 2). Any fish ascending a tributary in late summer-early autumn before rapidly descending it (within a week) and moving elsewhere in the catchment was discounted as a stray fish. Locations of Atlantic salmon tags were shown to predominate in the lower river in both years with a smaller number moving into the middle and upper Tweed as well as tributaries (Fig. 2). Tagged sea trout displayed a different pattern to salmon with sea trout moving into and occurring in more tributaries as well moving further up the Tweed system (Fig. 2). The Teviot appears to be a particularly important destination tributary for sea trout with regard to fish captured at Paxton in summer and early autumn.

Fig 2. Here

Adult sea trout and salmon migration speed through the lower half of the Tweed.

Sea trout and Atlantic salmon migration rates in the lower half of the Tweed (using AMR records from AMR 1 to AMR 3) were analysed using GLMMs. Using the model selection criteria two models were retained (Online resource 1). The selected model indicates a relationship between release date and the movement rate of salmon and sea trout, so those migrating earlier in the season had lower movement rates than those of later migrants, but with no effect of river flow or year. Sea trout also migrated at an elevated rate in comparison to salmon (General Linear Mixed effects Model - n=223, release date: estimate ± SE =0.027 ± 0.005, df=80.37,t=5.52, p<0.0001; species: estimate ± SE =0.529 ± 0.172,df=74.45, t=3.07,p<0.005; Fig. 3). However, the retention of a model without species included in the simpler model variants (model 5; Online resource 2) suggests that 'species' had a weaker effect than 'release date'.

Variation in adult sea trout and salmon migration throughout the River Tweed catchment.

The movement rates of salmon and sea trout was analysed on a broad spatial scale, with large-scale river reach rather than speeds between individual AMR pairings used in the models. The main stem was separated into three groups based on location within the study area: lower (Release - AMR 1 and AMR 1 - AMR 2), middle (AMR 2 - AMR 3, AMR 3 – AMR 4 and AMR 4 – AMR 5) and upper (AMR 5 - AMR 6 and AMR 6 - AMR 7) (Fig. 1). All the tributaries studied were combined in an effort to maximise sample size. The relationship between river reach and fish movement rate illustrates that adult salmon and sea trout migrated at a lower rate the further into the main river and tributaries they migrated (General Linear Mixed effects Model: n=392; Fig. 4, Table 2), unaffected by year or river reach flow. Sea trout moved at a higher rate in the lower and middle Tweed, whilst both species moved at similar rates in the upper Tweed and tributaries (Fig. 4, Table 2). Information concerning translation of relative (body lengths s^{-1}) and absolute (m s^{-1}) net travel speeds for different river reaches is presented in Table 3. Release date was, again, an important variable due to its inclusion in 50% of the initially selected models (Online resource 3). A General Linear Model (GLM) analysis of biological and environmental variables on the speed of migration into the tributaries and upper area of the Tweed showed that the groundspeed of adult salmonid migrants (adult sea trout and salmon, combined to increase sample size) moving from the main Tweed into the tributaries and upper Tweed was influenced by the discharge of the respective tributaries or upper section of the Tweed. Adults migrated at higher speeds when volumetric flow in the tributaries increased (Linear regression of log BL s^{-1} vs log flow: n=39, estimate ± SE = 0.2977 ± 0.1264, t=2.355, p<0.05).

Discussion

This study shows explicit differences in the spatial behaviour of summer and autumn-migrating Atlantic salmon and sea trout in the Tweed, both in terms of speed of movement through the lower and middle river, and in terms of the localities used for spawning, assuming that the track locations at the time of spawning indicate the spawning locations for tracked fish, an assumption made in most tracking studies where spawning is not explicitly observed (Aarestrup and Jepsen 1998; Finstad et al. 2005; Laughton and Smith 1992). Estimated mortality rates were 0-6% for sea trout and a maximum of 19% for salmon (but this figure includes regurgitation, which cannot be distinguished from mortality for intragastrically tagged salmon), while river drop-out rates were 3-8% for sea trout and 0% for salmon. These data suggest that over 80% of both Floy tagged salmon and sea trout are available for exploitation, yet exploitation rates of salmon are three times higher in the lower-middle river than for sea trout. The tracking data partially support the hypothesis that differences in migratory behaviour may account for recorded differences in exploitation rate in the lower-middle river, through altering their relative availability to anglers, but other factors such as angler behaviour, differential susceptibility to methods used, or differing reporting rates may also contribute to these differences (Gee 1980). It is also important to note the differences between the spatial bounds in the current study and the Tweed exploitation study (Table 1, Tweed Foundation

2015a). This also assumes that behaviour of tracked autumn-migrating sea trout and salmon is representative of the behaviour of conventionally tagged fishes in autumn over the much longer period of the exploitation study. Since there were low river-drop out and low post net-release mortality rates, the telemetry data provide valuable support for confidence in the T-bar tag estimates of exploitation rate and thus of fisheries management advice relating to the fishery. Telemetry data such as these provide an increasingly important complementary role in facilitating fisheries stock assessment, management and conservation (Clarke et al., 1991; Donaldson et al. 2008; Erkinaro et al. 1999; Webb, 1998).

Our study found that later running Atlantic salmon predominantly used the lower to middle sections of the main Tweed as an assumed spawning area. Conversely, later running sea trout widely used tributaries, especially the Teviot, and upper sections of the river. Sea trout moved faster than Atlantic salmon in the lower half of the river in relation to date of release. Earlier migrants of both species tended to migrate through the lower river slower than later released fish. Migration rates throughout the entire river system were highest in the main Tweed with speeds in river sections in the main river being consistently higher than in tributaries. Migration speeds for sea trout were fastest in the in the lower river and declined progressively through the middle and upper river with slowest movement between the main river and tributaries. By contrast, salmon moved quickly initially, slowed in the mid river and speeded up in the upper river. These results broadly agree with other research (Aarestrup and Jepsen 1998; Bagliniere et al. 1991; Bagliniere et al. 1990; Finstad et al. 2005; Östergren et al. 2011; Svendsen et al. 2004), with slowing in migration speed being due to switching between migration phases (Finstad et al. 2005; Økland et al. 2001). The markedly reduced migration rate within tributaries may also suggest why earlier migrants penetrate further into catchments (Östergren et al. 2011), but also highlights the effecs of river flow at this stage of migration (Svendsen et al. 2004; Thorstad and Heggberget 1998; Webb and Hawkins 1989). This current study is one of few (cf. Finstad et al. 2005) that has investigated the migratory behaviour of both Atlantic salmon and sea trout tagged within the same time periods and years, and from the same location, in relation to environmental variables as well as their estimated spawning positions within a large catchment.

In this study the estimated spawning position of Atlantic salmon and sea trout was spread widely at a catchment scale, despite relatively low rates of tag regurgitation and/or mortality, but differed between the species. However, Finstad et al. (2005) found that tracked Atlantic salmon and sea trout spawned within the same locality. It was also noted that fish tended to only migrate between 2-24 km to spawning locations in the River Lærdalselva, Norway (Finstad et al. 2005). However, the Tweed is considerably larger than the Lærdalselva, and the Tweed is not subject to severe winter icing that can restrict early and late runs by sea trout and salmon. In the Tweed most Atlantic salmon were tagged within the peak salmon run during August-September in both years and samples for earlier running fish were low. In some Scottish east coast salmon rivers earlier running salmon migrate further into the river system, which may explain why salmon tagged in the current study predominated within the lower-mid Tweed (Laughton 1989; Laughton and Smith 1992; Webb 1992). Spring Tweed salmon would be expected to migrate to upper reaches and tributaries, and is supported by historic T-bar tagging (R Campbell, unpublished data). Several studies have observed that female Atlantic salmon may select areas of river for spawning to influence density of juveniles during early life stages (Finstad et al 2013; Finstad et al 2010; Foldvik et al 2010). As such it is often observed that spawners distribute uniformly along a river length (Finstad et al 2013; Finstad et al 2010; Foldvik et al 2010). However, in some rivers clumping in spawners has been observed, possibly due to areas having limited connectivity (Finstad et al 2013; Finstad et al 2010; Foldvik et al 2010); the main stem Tweed has good longitudinal connectivity with few significant obstacles to large adult salmonids in that part of the river (Gauld et al. 2013).

Sea trout in the Tweed predominantly spawned within tributaries or the upper main channel (60-77% of fish detected). Studies in Swedish rivers found that sea trout spawning position varied between rivers with fish spawning in the main channel in some rivers whilst high numbers of fish spawned within tributaries (70%) in other rivers (Östergren et al. 2011). The apparent elevated use of the Teviot for spawning sea trout may be due to the fact that it is the largest sub-catchment of the Tweed at 1,137 km^2. The Teviot is comparable to the entire Upper Tweed in size (1007 km^2) and Is approximately double to quadruple the size of the other sub-catchments in the study, Ettrick (501 km^2), Gala (219 km^2), Leader (280 km^2), Till (668 km^2), Whiteadder (529 km^2). All of the sub-catchments included in the current study have high juvenile productivity with all of them showing high numbers during annual electrofishing surveys (Tweed Foundation, 2015b) The whole of the Tweed catchment supports salmon and / or trout spawning from the zone of tidal influence to minor headwaters, with a strong habitat segregation between salmon and trout, the former spawning in channels of more than 3 to 4 m and trout dominating elsewhere (Tweed Foundation, 2015b).

In the current study 82-88% of Atlantic salmon and 79-100% of sea trout were successfully tracked, moving from the release site, after being released. With intragastric tagging in Atlantic salmon there is an inherent risk of tag regurgitation, though it has often been regarded as low, and acceptable, given the perceived lower impact of the tagging method (Lucas and Baras 2000; Smith et al. 1998). The current study suggests that 9.8% of tags were regurgitated and/or in fish that died, all of which were 13 mm diameter tags. This estimate is likely an under- estimate due to the limited access for boat based tracking in areas upstream of the lower Tweed. Prior research on the Tweed has suggested regurgitation rates, based on recapture of double-tagged fish, are on average 14.8% (12.5-16.7%) which may explain a proportion of those salmon tagged for which no detections were made in the current study (Smith et al. 1998). As such the estimated spawning positions of salmon in the Tweed have a chance of error due to undocumented regurgitation/mortality beyond that already estimated (for example, where this occurred shortly before spawning time, since we used a longer threshold of the tag being static for over 2 months, without any subsequent recorded movement).

The salmon and sea trout angling season on the Tweed runs from 1st February to 30th November, demonstrating a wide range of river entry times for the different stocks – and some fish enter during the two month close season as well (R Campbell, unpublished data). Similarly broad timescales for river entry are observed in other rivers (Bij de Vaate et al. 2003; Jonsson and Jonsson 2002). The peak entry time of the sea trout in the Tweed estuary is in June and July (R. Campbell, unpublished data), which is also observed within the Rhine Delta, although migration peaks during August-October in several Danish rivers (K. Aarestrup, pers. comm.) and in higher latitude Norwegian Rivers (Jonsson and Jonsson 2002). Sea trout tagging dates ranged between July-September in 2010 and August to September in 2011 with the bulk of tagging occurring in September in both years meaning that tagged sea trout would be predominantly composed of late run fish in each year. The tagged fish being later migrants may explain why the River Teviot is the primarily used tributary as the River Till has a highly evident early and mid-summer run (R Campbell, unpublished data). Due to this, future research in the River Tweed should aim to tag sea trout over a greater time period to better represent early and peak running sea trout within samples.

In conclusion, the Tweed catchment is utilised differently by later-running Atlantic salmon and sea trout for spawning. The current study suggests that the majority of the main stem is utilised by salmon for spawning, whilst sea trout tended to use the upper catchment and tributaries for spawning. River dropouts and mortality for both sea trout and salmon were low in the current study, providing confidence in the current estimates of exploitation within the Tweed, and highlighting the utility of telemetry to test and validate elements of more conventional fisheries assessment methodology (Donaldson et al. 2008; Erkinaro et al. 1999; Metcalfe & Pawson, 2004; Webb 1998).

Acknowledgements

This work was supported by the Living North Sea project and the Interreg IVB North Sea Region Programme. We thank the landowners, river boatmen and angling clubs involved in the work for allowing us to place logging equipment in their waters as well as their help and advice. We also thank River Tweed Commission Bailiffs Alan Davidson, Eric Hastings and Kenny Graham for help retrieving logging equipment from the estuary. Thanks are also due to Nick Yonge, Fay Hieatt, James Hunt and Kenny Galt at the Tweed Foundation for their help and support during this work.

References

Aarestrup, K. & N. Jepsen, 1998. Spawning migration of sea trout (*Salmo trutta* (L)) in a Danish river. Hydrobiologia 371: 275-281.

Bagliniere, J., G. Maisse & A. Nihouarn, 1991. Radio-tracking of male adult Atlantic salmon, *Salmo salar* L., during the last phase of spawning migration in a spawning stream (Brittany, France). Aquatic Living Resources 4: 161-167.

Bagliniere, J. L., G. Maisse & a. Nihouarn, 1990. Migratory and reproductive behaviour of female adult Atlantic salmon, *Salmo salar* L., in a spawning stream. Journal of Fish Biology 36: 511-520.

Bates, D., M. Maechler, B. Bolker & S. Walker, 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.

Bendall, B., A. Moore, D. Maxwell, P. Davison, N. Edmonds, D. Archer, D. Solomon, V. Greest, R. Wyatt & K. Broad, 2012. Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. Fisheries Management and Ecology 19: 475-483.

Bij de Vaate, A., A. W. Breukelaar, T. Vriese, G. De Laak & C. Dijkers, 2003. Sea trout migration in the Rhine delta. Journal of Fish Biology 63: 892-908.

Bunt, D.A., 1991. Use of rod catch effort data to monitor migratory salmonids in Wales. In: Cowx, I.G. (ed.) Catch Effort Sampling Strategies: Their Application in Freshwater Fisheries Management. Fishing News Books, Oxford: 15-32.

Butler, J.R.A., A. Radford, G. Riddington & R. Laughton, 2009. Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland. The economic impact of recreational rod fisheries. Fisheries Research 96: 259-266.

Cefas, Environment Agency and Natural Resources Wales, 2014. Annual assessment of salmon stocks and fisheries in England and Wales 2013. Available at: www.cefas.defra.gov.uk/publications/files/SalmonReport2013-final.pdf

Clarke, D., W.K. Purvis & D. Mee, 1991. Use of telemetric tracking to examine environmental influence on catch effort indices. A case study of Atlantic salmon (*Salmo salar* L.) in the River Tywi, South Wales. In: Cowx, I.G. (ed.) Catch Effort Sampling Strategies: Their Application in Freshwater Fisheries Management. Fishing News Books, Oxford: 33-48.

Currie, J., 1997. Pollution prevention on the River Tweed: past, present and future. Science of the Total Environment 194-195: 147-154.

Davey, C. & M. Lapointe, 2007. Sedimentary links and the spatial organization of Atlantic salmon (*Salmo salar*) spawning habitat in a Canadian Shield river. Geomorphology 83: 82-96.

Donaldson, M.R., R. Arlinghaus, K.C. Hanson & S.J. Cooke, 2008. Enhancing catch-and release science with biotelemetry. Fish and Fisheries 9: 79-105.

Erkinaro, J., F. Økland, K. Moen & E. Niemelä, 1999. Return migration of the Atlantic salmon in the Tana River: distribution and exploitation of radiotagged multi-sea-winter. Boreal Environment Research 4: 115-124.

Everest, J., T. Bradwell & N. Golledge, 2005. Subglacial landforms of the Tweed palaeo-ice stream. Scottish Geographical Journal 121: 163-173.

Fausch, K. D., C. E. Torgersen, C. V. Baxter & H. W. Li, 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes a continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. Bioscience 52: 483-498.

Finstad, A. G., L. M. Sættem & S. Einum, 2013. Historical abundance and spatial distributions of spawners determine juvenile habitat accessibility in salmon: implications for population dynamics and management targets. Canadian Journal of Fisheries and Aquatic Sciences 70: 1339-1345.

Finstad, A. G., S. Einum, L. M. Sættem & B. A. Hellen, 2010. Spatial distribution of Atlantic salmon (*Salmo salar*) breeders: among- and within-river variation and predicted consequences for offspring habitat availability. Canadian Journal of Fisheries and Aquatic Sciences 67: 1993-2001.

Finstad, A., F. Økland, E. Thorstad & T. Heggberget, 2005. Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. Journal of Fish Biology 67: 919-930.

Foldvik, A., A. G. Finstad & S. Einum, 2010. Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. Journal of Animal Ecology 79: 501-509.

Gardiner, R., 1989. Tweed juvenile salmon and trout stocks. In: Mills, D. (ed) Tweed towards 2000. The Tweed Foundation, Melrose, 105-114.

Gauld, N.R., R.N.B. Campbell & M.C. Lucas, 2013. Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. Science of the Total Environment 458-460: 435-443.

Gee, A.S., 1980. Angling success for Atlantic salmon (*Salmo salar*) in the River Wye in relation to effort and flows. Fisheries Management 11: 131-138.

Gerlier, M. & P. Roche, 1998. A radio telemetry study of the migration of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta trutta* L.) in the upper Rhine. Hydrobiologia 371: 283-293.

Hawkins, A. D. & G. W. Smith, 1986. Radio-tracking observations on Atlantic salmon ascending the Aberdeenshire Dee. Scottish fisheries research report 36, 24pp. Scottish Office, Edinburgh.

Jonsson, N. & B. Jonsson, 2002. Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. Freshwater Biology 47: 1391-1401.

Kennedy, R. J., I. Moffett, M. M. Allen & S. M. Dawson, 2013. Upstream migratory behaviour of wild and ranched Atlantic salmon *Salmo salar* at a natural obstacle in a coastal spate river. Journal of Fish Biology 83: 515-530.

Kuznetsova, A., P. B. Brockhoff, R. H. B. Christensen & 2014. lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-20. http://CRAN.R-project.org/package=lmerTest

Laughton, R., 1989. The Movements of Adult Salmon within the River Spey. Scottish fisheries research report 41. Scottish Office, Edinburgh.

Laughton, R. & G. W. Smith, 1992. The relationship between the date of river entry and the estimated spawning position of adult Atlantic salmon (*Salmo salar* L.) in two major Scottish east coast rivers. In Priede, I. G. & S. M. Swift (eds) Wildlife Telemetry. Ellis Horwood, New York: 423-433.

Lucas, M. C. & E. Baras, 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish and Fisheries 1: 283-316.

Lucas, M. C. & E. Baras, 2001. Migration of Freshwater Fishes. Blackwell Science Oxford, Oxford; Malden, MA.

Metcalfe, J.D. & M.G. Pawson, 2004. Measuring fish behaviour: the relavance to the managed exploitation of shared stocks. In Payne, A.I.L., C.M. O'Brien, & S.I Rogers (eds). Blackwell, Oxford: 303-315.

Økland, F., J. Erkinaro, K. Moen, E. Niemelä, P. Fiske, R. S. McKinley & E. B. Thorstad, 2001. Return migration of Atlantic salmon in the River Tana: Phases of migratory behaviour. Journal of Fish Biology 59: 862-874.

Östergren, J., H. Lundqvist & J. Nilsson, 2011. High variability in spawning migration of sea trout, *Salmo trutta*, in two northern Swedish rivers. Fisheries Management and Ecology 18: 72-82.

Potter, E.C.E., J.C. Maclean, R.J. Wyatt & R.N.B. Campbell, 2003. Managing the exploitation of migratory salmonids. Fisheries Research 62: 127-142.

Primmer, C., A. Veselov, A. Zubchenko, A. Poututkin, I. Bakhmet & M. Koskinen, 2006. Isolation by distance within a river system: genetic population structuring of Atlantic salmon, *Salmo salar*, in tributaries of the Varzuga River in northwest Russia. Molecular Ecology 15: 653-666.

R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Richards, S. A., 2008. Dealing with overdispersed count data in applied ecology. Journal of Applied Ecology 45: 218-227.

Scarnecchia, D.L. & B.B. Roper, 2000. Large-scale differential summer habitat use of three anadromous salmonids in a large river basin in Oregon, USA. Fisheries Management and Ecology 7: 197-209.

Schaller, H. A., C. E. Petrosky & O. P. Langness, 1999. Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. Canadian Journal of Fisheries and Aquatic Sciences 56: 1031-1045.

Sheail, J., 1998. The Tweed fisheries: An historical perspective. Science of the Total Environment 210: 469-482.

Smith, G. W., R. N. B. Campbell & J. S. MacLaine, 1998. Regurgitation rates of intragastric transmitters by adult Atlantic salmon (*Salmo salar* L.) during riverine migration. Hydrobiologia 371-372: 117-121.

Stewart DC, Smith GW & Youngson AF (2002) Tributary-specific variation in timing of return of adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. Canadian Journal of Fisheries and Aquatic Sciences, 59:276-281.

SQW Ltd, 2006. Economic impact from angling on the Tweed river system. A report to the River Tweed Commissioners, Melrose.

Svendsen, J., A. Koed & K. Aarestrup, 2004. Factors influencing the spawning migration of female anadromous brown trout. Journal of Fish Biology 64: 528-540.

Thorley, J.L., A.F. Youngson & R. Laughton, 2007. Seasonal variation in rod recapture rates indicates differential exploitation of Atlantic salmon, *Salmo salar*, stock components. Fisheries Management and Ecology 14: 191-198.

Thorstad, E. & T. Heggberget, 1998. Migration of adult Atlantic salmon (*Salmo salar*); the effects of artificial freshets. Hydrobiologia 371-372: 339-346.

Thorstad, E. B., F. Økland, K. Aarestrup & T. G. Heggberget, 2008. Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. Reviews in Fish Biology and Fisheries 18: 345-371.

Tweed Foundation, 2015a. Tweed Foundation Methods. In. http://www.tweedfoundation.org.uk/html/methods.html. Accessed 04/05/2015.

Tweed Foundation, 2015b. Tweed Foundation Reports. In. http://www.tweedfoundation.org.uk/html/reports.html. Accessed 05/05/2015.

Webb, J., 1989. The Movements of Adult Atlantic Salmon in the River Tay. Scottish fisheries research report 44. Scottish Office, Edinburgh. 32 pp.

Webb, J., 1990. The Behaviour of Adult Atlantic Salmon Ascending the Rivers Tay and Tummel to Pitlochry Dam. Scottish fisheries research report 48. Scottish Office, Edinburgh. 27 pp.

Webb, J., 1992. The Behaviour of Adult Salmon (*Salmo salar* L.) in the River Tay as Determined by Radio Telemetry. Scottish fisheries research report 52. Scottish Office, Edinburgh.

Webb J.H. 1998. Catch and Release: the Survival and Behaviour of Atlantic salmon Angled and Returned to the Aberdeenshire Dee, in Spring and Early Summer. Scottish Fisheries Research Report 62, Fisheries Research Services and The Atlantic Salmon Trust, Edinburgh. 16 pp.

Webb, J. & A. D. Hawkins, 1989. The Movements and Spawning Behaviour of Adult Salmon in the Girnock Burn, A Tributary of the Aberdeenshire Dee , 1986. Scottish fisheries research report 40. Scottish Office, Edinburgh, 41 pp.

Figure captions

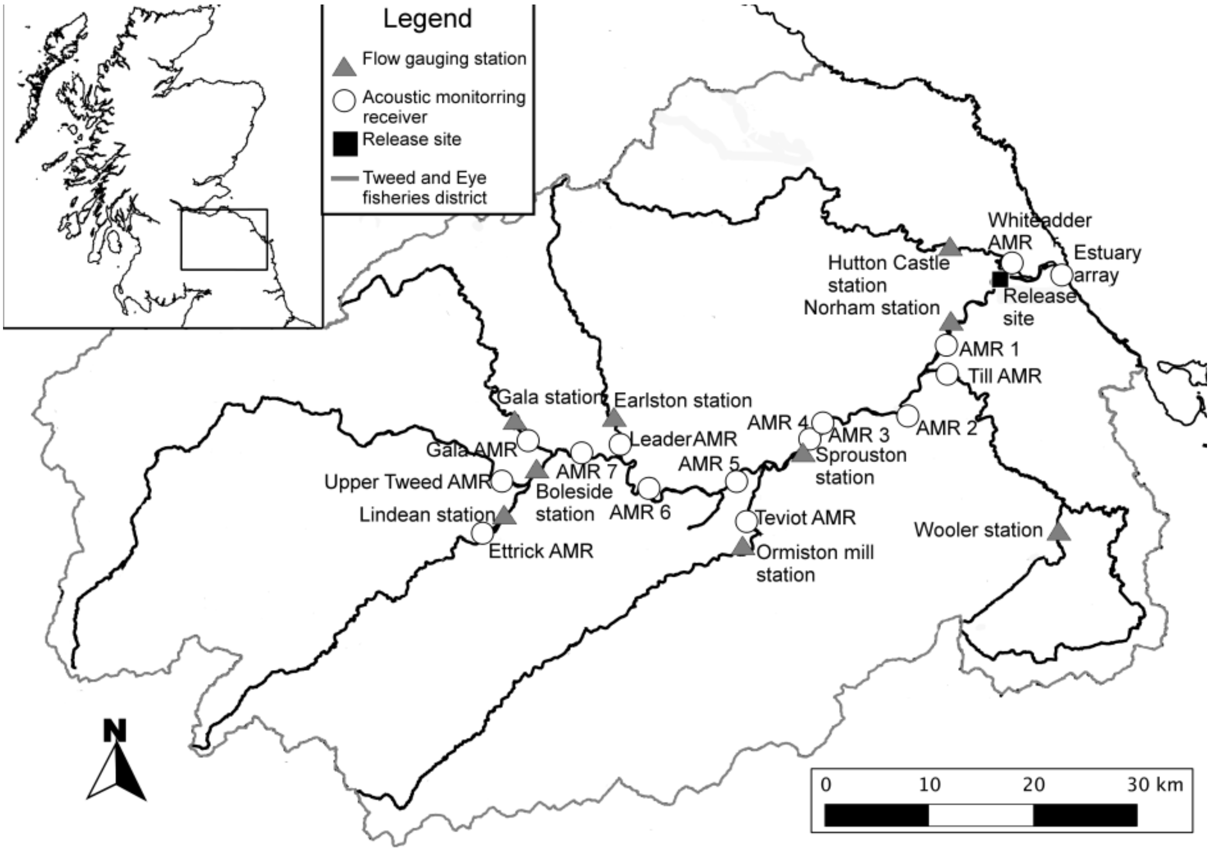


Fig. 1: Map of the study area.

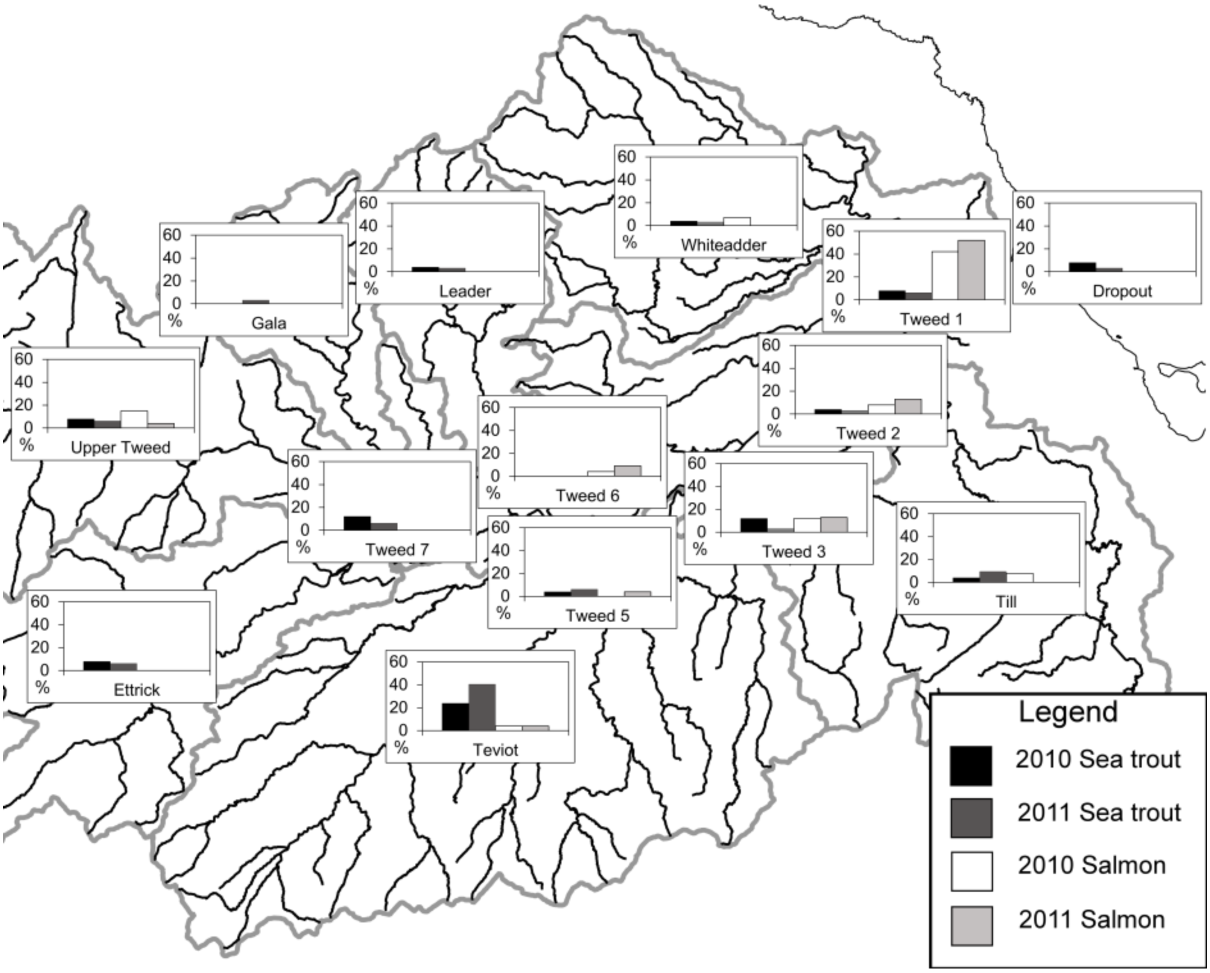
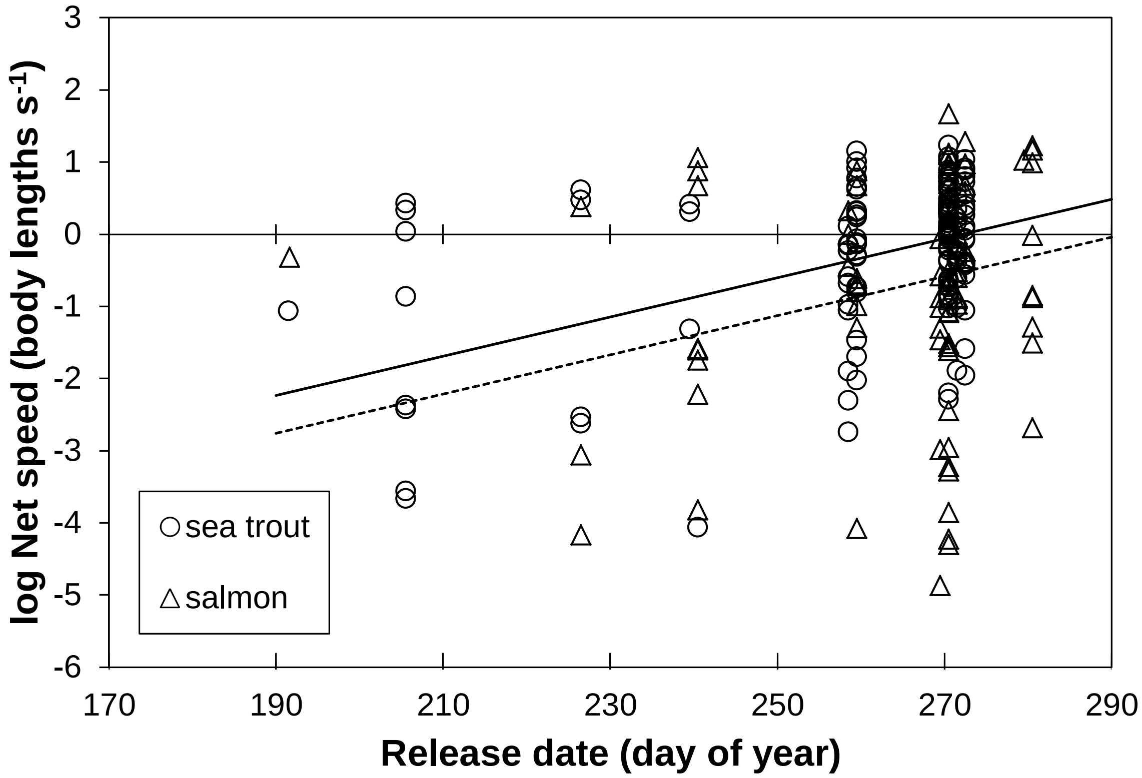


Fig. 2: Map of the end destination for sea trout and salmon in 2010 and 2011, including the proportion of each run last detected in each area.



569

570 **Fig. 3:** The relationship between release date and the movement rates of adult Atlantic

571 salmon and sea trout. Solid black lines represent sea trout and dashed black lines represent

572 salmon.

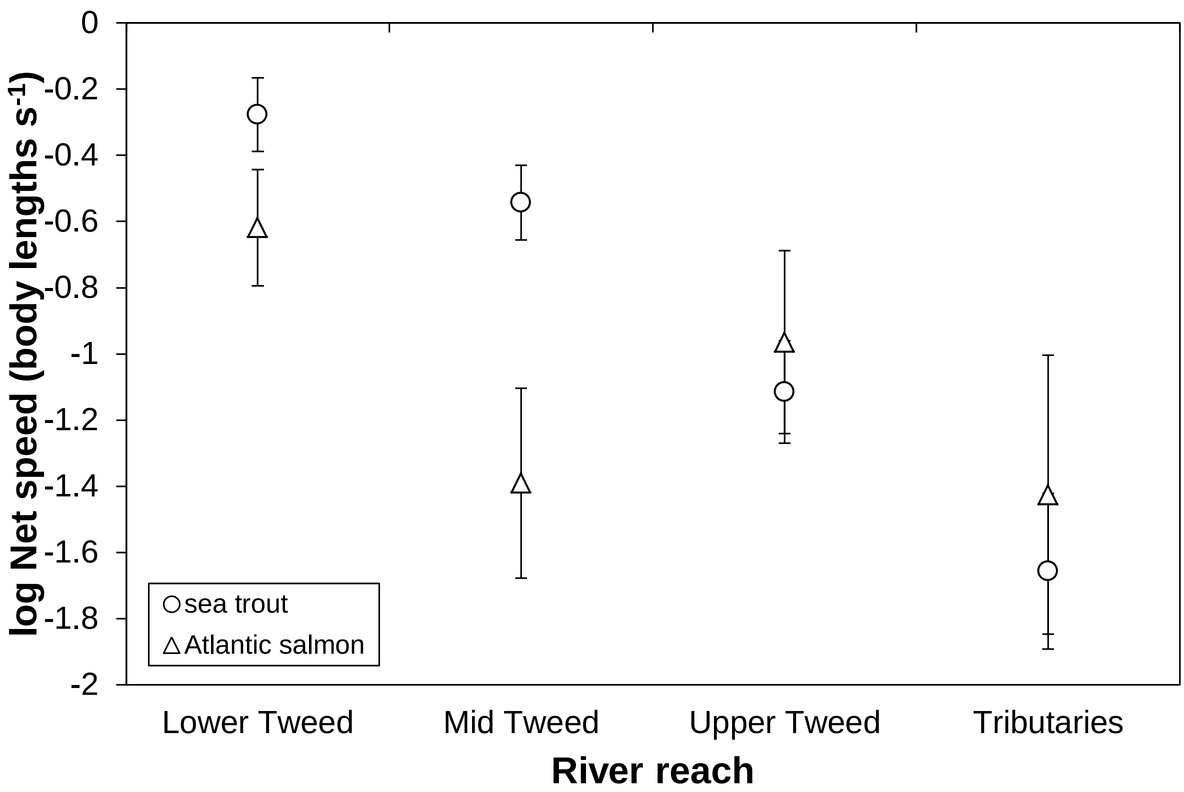


Fig. 4: The 2010-2011 movement rates of adult sea trout and Atlantic salmon combined in relation to position within the River Tweed catchment. Error bars display the standard error of the mean.

Table 1: Summary of the exploitation rates of Atlantic salmon and sea trout within the Tweed catchment during the spring (Feb – May), summer (Jun – Aug) and autumn (Sep – Nov) fishing seasons. Exploitation data represents catches from 1994-2011.

	Lower	Middle	Upper	Tributaries	Total Tagged	Total Recaptured
Spring salmon	50.0%	21.4%	7.1%	21.4%	58	14
Summer salmon	57.1%	28.6%	0.0%	14.3%	129	7
Autumn salmon	54.3%	20.0%	14.3%	11.4%	791	35
Total annual salmon	53.6%	21.4%	10.7%	14.3%	978	56
Spring sea trout	-	-	-	-	3	0
Summer sea trout	0.0%	33.3%	0.0%	66.7%	79	3
Autumn sea trout	10.0%	40.0%	40.0%	10.0%	581	10
Total annual sea trout	7.7%	38.5%	30.8%	23.1%	663	13

Table 2: Coefficients of the selected GLMM (reach, species variables) for migration speeds of sea trout and Atlantic salmon through the reaches and tributaries of the Tweed.

	Estimate (±SE)	Residual *df*	*t*	*p*
Intercept	-2.3702 ± 0.1315	163.3	-4.53	<0.0001
Reach - Mid	-0.4361 ± 0.1345	339.2	-3.23	<0.01
Reach - Trib	-1.2118 ± 0.2062	346.5	-6.02	<0.0001
Reach - Upper	-0.8898 ± 0.1773	370.4	-4.94	<0.0001
Species - sea trout	0.6571 ± 0.1598	95.8	2.03	<0.0001

Table 3: The movement rates of sea trout and salmon moving through each reach of the Tweed catchment in 2010-2011. Table denotes movement rates converted between relative speeds (BL s^{-1}) and absolute speeds (m s^{-1}) as well as mean fish size and sample sizes of fish moving in each river section.

River reach & Species	Sample size	Mean length (mm) ± SE	Mean net movement rate (log BL s^{-1}) ± SE	Mean net movement rate (BL s^{-1}) ± SE	Mean net speed (m s^{-1}) ± SE
Lower salmon	74	672.36 ± 15.89	-1.02 ± 0.07	0.17 ± 0.02	0.12 ± 0.01
Mid salmon	34	651.76 ± 16.92	-1.34 ± 0.12	0.13 ± 0.03	0.09 ± 0.02
Upper salmon	16	684.38 ± 28.17	-1.19 ± 0.12	0.1 ± 0.02	0.07 ± 0.01
Tributaries salmon	6	622.5 ± 43.93	-1.31 ± 0.15	0.06 ± 0.02	0.04 ± 0.02
Total salmon	141	663.12 ± 10.24	-1.17 ± 0.05	0.14 ± 0.01	0.1 ± 0.01
Lower sea trout	96	571.51 ± 6.5	-0.74 ± 0.05	0.25 ± 0.02	0.15 ± 0.01
Mid sea trout	91	576.04 ± 6.93	-0.86 ± 0.05	0.21 ± 0.02	0.12 ± 0.01
Upper sea trout	43	585 ± 11.54	-1.12 ± 0.06	0.11 ± 0.07	0.07 ± 0.01
Tributaries sea trout	32	565.16 ± 9.05	-1.31 ± 0.1	0.09 ± 0.05	0.05 ± 0.01
Total sea trout	268	573.28 ± 4	-0.94 ± 0.03	0.19 ± 0.01	0.11 ± 0.01

Supplementary material

Online resource 1: Summary of number of fish caught and tagged on each day of netting at Paxton during 2010 and 2011.

Species	Tagging date	Number tagged	Fork Length [mean ± SD (range), mm]	Weight [mean ± SD (range), kg]*	Tag to body weight ratio [mean (range), %]
Salmon	12/06/2010	1	695.0	3.2	0.27
Salmon	10/07/2010	3	546.7 ± 47.3 (510–600)	2 ± 0.2 (1.8–2.2)	0.45 (0.4–0.47)
Salmon	24/07/2010	2	602.5 ± 17.7 (590–615)	2.2 ± 0.13 (2.2–2.4)	0.39 (0.38–0.41)
Salmon	14/08/2010	4	553.8 ± 44.2 (500–590)	2 ± 0.16 (1.9–2.2)	0.44 (0.41–0.48)
Salmon	28/08/2010	10	599.0 ± 101.3 (500–850)	2.6 ± 1.35 (1.9–6.3)	0.39 (0.14–0.48)
Salmon	06/09/2010	3	660.0 ± 224.7 (475–910)	4 ± 3.43 (1.9–7.9)	0.33 (0.11–0.47)
Salmon	27/09/2010	10	732.0 ± 102.7 (595–940)	4.2 ± 2 (2–8.9)	0.25 (0.1–0.41)
Salmon	28/09/2010	7	705.0 ± 63.7 (605–785)	3.5 ± 0.92 (2.3–4.8)	0.27 (0.19–0.4)
Salmon	29/09/2010	6	863.3 ± 133.4 (625–990)	7.2 ± 3 (2.4–10.6)	0.16 (0.8–0.38)
Salmon	07/10/2010	5	567.0 ± 44.5 (500–610)	2.1 ± 0.18 (1.9–2.3)	0.43 (0.39–0.48
Salmon	Total 2010	51	666.6 ± 134.5 (475–990)	3.5 ± 2.24 (1.9–10.6)	0.33 (0.8–0.48
sea trout	26/06/2010	3	525.0 ± 13.2 (510–535)	1.9 ± 0.02 (1.8–1.9)	0.47 (0.47–0.48
sea trout	10/07/2010	4	536.3 ± 22.5 (510–555)	1.9 ± 0.05 (1.8–1.9)	0.46 (0.45–0.48)
sea trout	24/07/2010	6	541.7 ± 24 (510–570)	1.9 ± 0.07 (1.8–2)	0.46 (0.44–0.48)
sea trout	14/08/2010	3	495.0 ± 72.6 (420–565)	2 ± 0.11 (1.8–2.1)	0.45 (0.43–0.48)
sea trout	28/08/2010	1	470	1.9	0.47
sea trout	27/09/2010	10	577.0 ± 40 (520–660)	2.1 ± 0.27 (1.8–2.8)	0.42 (0.32–0.47)
sea trout	28/09/2010	3	546.7 ± 46.2 (520–600)	2 ± 0.2 (1.8–2.2)	0.45 (0.4–0.48)
sea trout	29/09/2010	3	576.7 ± 25.2 (550–600)	2.1 ± 0.13 (1.9–2.2)	0.43 (0.4–0.46)
sea trout	Total 2010	33	547.4 ± 44.4 (420–600)	2 ± 0.18 (1.8–2.8)	0.45 (0.32–0.48
Salmon	15/09/2011	1	540	1.9	0.47
Salmon	16/09/2011	9	663.9 ± 93.7 (490–765)	3.1 ± 0.98 (1.8–4.4)	0.31 (0.2–0.48)
Salmon	26/09/2011	4	527.5 ± 56.2 (455–585)	1.9 ± 0.1 (1.9–2.1)	0.45 (0.42–0.47
Salmon	27/09/2011	10	712.0 ± 110.9 (520–880)	3.9 ± 1.5 (1.9–7.1)	0.28 (0.13–0.48)
Salmon	28/09/2011	3	736.7 ± 161.7 (550–830)	4.5 ± 2.24 (1.9–5.8)	0.26 (0.15–0.46)
Salmon	29/09/2011	1	500	1.9	0.48
Salmon	Total 2011	28	659.1 ± 121.4 (455–880)	3.3 ± 1.48 (1.9–7.1	0.32 (0.13–0.48)
sea trout	27/08/2011	1	550	1.9	0.46
sea trout	15/09/2011	6	535.0 ± 33.3 (500–580)	1.9 ± 0.09 (1.9–2.1)	0.46 (0.43–0.48)
sea trout	16/09/2011	8	621.3 ± 61.7 (560–760)	2.5 ± 0.75 (2–4.3)	0.37 (0.2–0.45)
sea trout	27/09/2011	8	593.8 ± 60.1 (535–700)	2.3 ± 0.54 (1.9–3.3)	0.4 (0.27–0.47)
sea trout	28/09/2011	3	513.3 ± 41.6 (480–560)	1.9 ± 0.07 (1.9–2)	0.47 (0.45–0.48)
sea trout	29/09/2011	6	569.2 ± 97.2 (495–730)	2.3 ± 0.78 (1.9–3.8)	0.41 (0.24–0.48)
sea trout	Total 2011	32	576.1 ± 69.6 (480–760)	2.3 ± 0.59 (1.9–4.3)	0.42 (0.2–0.48)

*Weight (lb) estimated from length (cm) using the local Tweed salmonid length to weight calculation ($y = 0.008x^2 - 0.7991x + 24.09$, $R^2 = 0.98716$) and then converted into kilograms.

Online resource 2: Candidate General Linear Mixed Models for the migration speeds of sea trout and Atlantic salmon migrating through the lower half of the River Tweed. Table displays all variables used in each model as well as summary data for each model, "+" symbols represent the inclusion of a variable as a factor.

Model	Intercept	Year	Flow	Release date	River Section	Species	Flow : River section	Flow : Species	Species : Release date	df	AIC	Delta
21*	-7.928			0.02719		+				5	723.	0
5	-7.219			0.02566						4	728	4.73

* Selected model.

Online resource 3: Candidate General Linear Mixed Models for the migration speeds of sea trout and Atlantic salmon migrating through the reaches and tributaries of the Tweed. Table displays all variables used in each model as well as summary data for each model.

Mode l	Intercep t	River reach	Release date	Species	Year	Flow	Species : Flow	Year : Flow	df	AIC	delta (Δ)
8	-5.555	+	0.01852	+					8	1283.5	0
4	-5.008	+	0.01737						7	1286.4	2.92
6*	-0.6483	+		+					7	1288	4.53
2	-0.4518	+							6	1288.3	4.88

*Candidate model